

## HEAT REGULATION IN SOME ARCTIC AND TROPICAL MAMMALS AND BIRDS \*

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In the preceding paper are presented observations and measurements of the body insulation of a series of arctic and tropical mammals and birds. In the present paper we shall describe experiments in which our animals were subjected to gradually lowered air temperatures in a respiration chamber, where the heat production was simultaneously determined through the oxygen consumption or carbon dioxide production. Similar experiments have been conducted earlier on many laboratory mammals and birds and a few wild animals. Excellent data were obtained by Theodor (1878), Falloise (1900), Rubner (1902), Martin (1902), Goto (1923), Terroine and Trautmann (1927), Benedict and MacLeod (1929), Giaja (1931), Kayser (1930, 1937), Benedict and Fox (1933), Gelineo (1934), Swift and Forbes (1939), Kendeigh (1939, 1944), Kalabukhov (1940), and Herrington (1940).

From the earliest investigations it was made clear that down to a certain environmental temperature (the critical temperature) the body temperature could be maintained, without increasing the metabolism, simply by increasing the insulation (so-called physical heat regulation). Below the critical temperature the body temperature could be maintained only by increasing the heat production (so-called metabolic or "chemical" heat regulation). For geese and rabbits it was found that the critical temperature could be as low as 0° C., and from observed fact that eskimo dogs sleep on the snow at -40° C. or below we could expect to find arctic mammals having a critical temperature that low or even lower. It was considered likely that cold experiments on tropical mammals and birds would furnish a valuable contrast to our arctic material, and through the courtesy of the Navy we were granted a six months stay in the Panama Canal Zone for the study of this and other problems.

### ANIMAL MATERIAL

The following arctic mammals were used in our experiments at Point Barrow, Alaska, latitude 71° N.:

White fox ( <i>Alopex lagopus</i> )	Lemming ( <i>Dicrostonyx groenlandicus rubricatus</i> )
Eskimo dog ( <i>Canis familiaris</i> )	Weasel ( <i>Mustela rixosa</i> )
Polar bear cubs ( <i>Thalarctos maritimus</i> )	
Ground squirrel ( <i>Citellus parryii</i> )	

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and the following birds:

Arctic gull (*Larus hyperboreus*)                      Snow bunting (*Plectrophenax nivalis*)  
 Canada jay (*Perisoreus canadensis*)

The dogs, foxes, and polar bear cubs were kept in outdoor wire cages at an average temperature of  $-25^{\circ}$  C. The weasels, lemmings, and ground squirrels were kept in an animal house at around  $-10^{\circ}$  C. to  $+5^{\circ}$  C. These small animals all built nests into which they could retire and in which they spent most of their time. The gulls and snow buntings were caught near the laboratory in September and were kept outside in wire cages. Normally they migrate south during the winter. The jays were caught 200 miles south of the laboratory in April. All of the animals outdoors had access to indoor nest boxes through openings in the wall of the animal house; these, however, they seldom used, even at temperatures  $-40^{\circ}$  C. or below.

The tropical mammals and birds used for our cold experiments were all caught in the Canal Zone (Panama) and were kept in wire cages at the Barro Colorado Island laboratory (latitude  $9^{\circ}$  N.) where the outdoor temperature is usually  $25^{\circ}$  C to  $30^{\circ}$  C.

The following tropical mammals were obtained and used:

Two-toed sloth (*Choloepus hoffmanni*)      Raccoon (*Procyon cancrivorus*)  
 Night monkey (*Aotus trivirgatus*)          Coati (*Nasua narica*)  
 Marmoset (titi) (*Leontocebus geoffroyi*)      Jungle rat (*Proechimys semispinosus*)

and the following tropical birds:

Manakin (*Pipra mentalis*)                      Night hawk (Paurangue) (*Nyctidromus albicollis*)

#### EXPERIMENTAL

In order to be able to compare the effect of temperature on the metabolism in widely different mammals and birds we have referred to the average metabolic level at rest as 100, determined as  $O_2$  consumption or  $CO_2$  production in the thermo-neutral zone (= temperature zone of lowest metabolism). All changes are given in relation to that figure.

The arctic animals were studied during the winter of 1947-1948 in an interrupted sequence for each animal, in such a way, however, that each animal covered the whole range of temperatures. The basal reference level of heat expenditure could therefore be established empirically for each individual, which eliminated the uncertainty involved in correcting the metabolism for differences in weight. The animals were given a one to two hour period in the chamber at the proper temperature before a series of determinations was made, extending over another period of one to three hours.

The tropical mammals and birds could withstand only a relatively small range of external temperatures and each individual could therefore be run through the whole temperature range in a single day, starting at room temperature and thereafter going down step by step. The animal usually remained in the respiration chamber for eight to twelve hours, with about two hours at each temperature and allowing one hour for bringing the temperature down.

## APPARATUS

A wooden box was mounted outside one of the windows of the laboratory at Point Barrow. The box was furnished with a window facing the laboratory window and was equipped with a fan and a resistance controlled electric heater. The box could be maintained at any temperature warmer than the outside air. The animal was placed on top of a narrow piece of plywood in a wire screen cage just large enough to hold it without cramping. The cage was placed on a pan furnished with a narrow well containing a non-freezing glycerine solution. Over the cage was put a closely fitting sheet metal respiration chamber resting with its lower edge in the glycerine well to form an airtight seal. The chamber carried tygon tubes for in- and outgoing air and a thermometer. The chamber air was adjusted to the proper

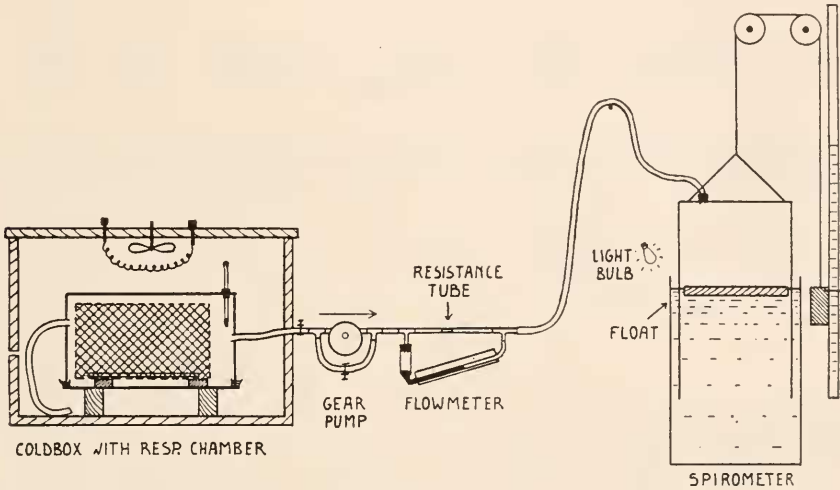


FIGURE 1. Open circuit metabolism apparatus used in the cold experiments. A wooden float covered with sheet metal protects the water from gas diffusion. The light bulb keeps the spirometer gases well stirred by setting up convection currents.

temperature by regulating the box temperature. It is realized that the air temperature in a small respiration chamber is not an ideal way of characterizing the environmental heat situation. However, it is comparable to all other similar experiments.<sup>6</sup> Heat loss by evaporation was always low because of high relative humidity in the small respiration chamber.

Outdoor air, prewarmed in the wooden box, entered the respiration chamber through a six-foot length of tubing. Air was exhausted from the chamber at the other end by means of a small gear pump which propelled it through a flow meter into a respirometer. The speed of the gear pump and the shunt was adjusted so as to give a ventilation through the chamber which would maintain the carbon dioxide of the exhaust air at about 1 per cent, as checked by gas analysis. As our animals varied greatly in weight and metabolic rates, we needed three sizes of

<sup>6</sup> In his classical work, Martin (1902) gives only the waterbath temperatures. The air temperature in his glass respiration chamber might have been considerably warmer.

spirometers and respiration chambers, two sizes of gear pumps and different bore plastic resistance tubes in the flow meter in order to maintain the same degree of accuracy throughout the series.

Small mammals or birds were usually placed on a narrow piece of plywood in two small tin cans taped together at the openings and furnished with the necessary tubes for in- and outgoing air and temperature measurements. The ventilation was measured on the spirometer and samples were taken out for analysis using either the  $\frac{1}{2}$  cc. analyzer (Scholander, 1947) for  $\text{CO}_2$  and  $\text{O}_2$ , or in Panama, the Haldane apparatus for  $\text{CO}_2$ . A light bulb on one side of the spirometer kept the gases well

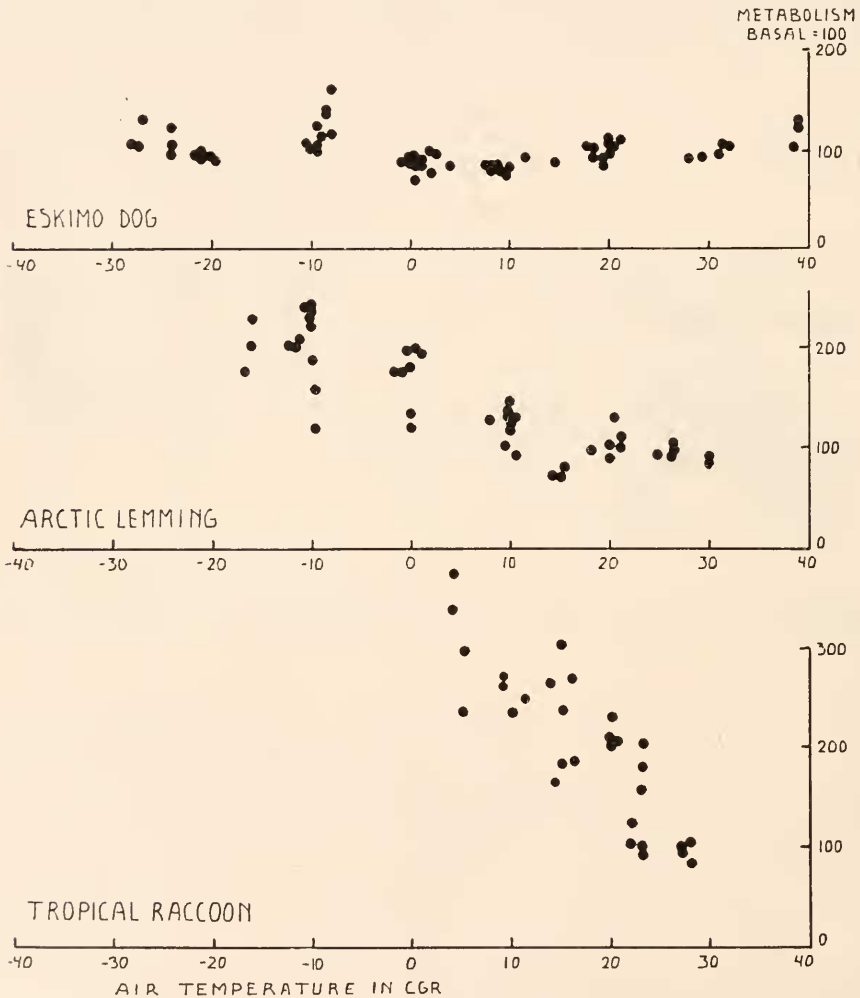


FIGURE 2. Effect of environmental temperature on the metabolic rate in eskimo dog, arctic lemming, and tropical raccoon expressed in terms of basal metabolic rate = 100. The steepness of the curves describes the relative temperature sensitivity of the animal but does not correlate with the weight of the animals or with their body insulation.

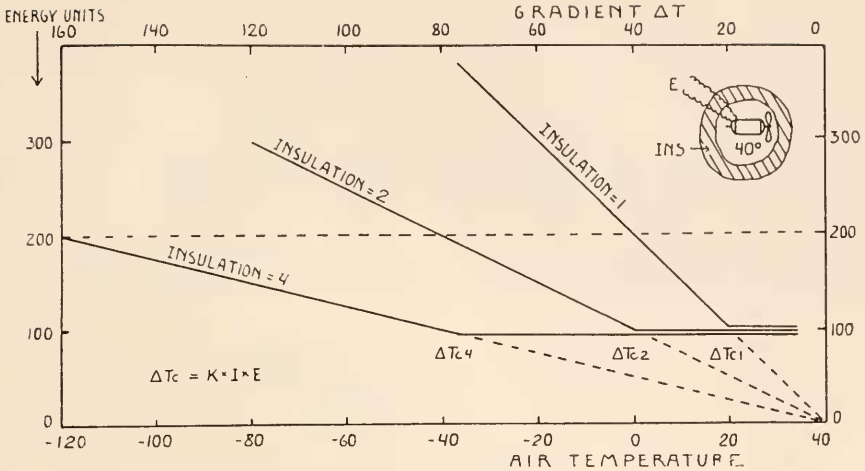


FIGURE 3. Diagram of a thermoregulated system consisting of an electric fan inside a rigid insulator (insert). The full drawn lines represent the relative energy input necessary to maintain the "body temperature" of 40° C. for different air temperatures, assuming a minimum (basal) energy level of 100 and a maximum insulation of 1, 2, and 4 units. The thermoregulation is assumed to proceed in two steps: first an increase in insulation until it reaches maximum at the critical temperature, then an increase in the metabolic rate. At the critical temperature the body-to-air gradient is called the critical gradient  $\Delta T_c$ . At constant insulation the system cools proportionally to the gradient and it will be seen from the figure that the critical gradient is proportional to both insulation and metabolic rate according to the equation given.

stirred by setting up slight convection currents in the spirometer. The accuracy obtained by this well established open circuit technique was ample for our purpose.

For cooling the tropical animals, a deep freeze box was used with an insulated wooden lid furnished with fan and heater. In this was placed the respiration chamber as already described.

The rate of oxygen consumption (arctic animals) or  $\text{CO}_2$  production (tropical animals) relative to temperature was plotted for each individual animal, the basal level taken from the plot, and the data recalculated and replotted relative to the basal level which is called 100 (Figs. 2-11).

In the large series of arctic experiments performed by Hock, both  $\text{CO}_2$  production and oxygen consumption were determined. The  $\text{RQ}$  was rarely outside 0.70-0.85 all through the temperature ranges, and hence either oxygen consumption or  $\text{CO}_2$  production can be taken as proportional to the heat production, and either one can accurately enough serve our purpose to describe relative changes in heat production.

#### THEORETICAL CONSIDERATIONS

It became clear from the very beginning of these experiments that the larger arctic mammals like the fox and dog did not need to increase their heat production to stand the relatively modest temperature of  $-30^\circ \text{C}$ . that we were able to offer them, and that their metabolism remained essentially unchanged from  $+30^\circ \text{C}$ . to  $-30^\circ \text{C}$ . However, the smaller arctic mammals and birds soon reacted by slowly increasing their metabolism with falling temperature.

# ARCTIC MAMMALS

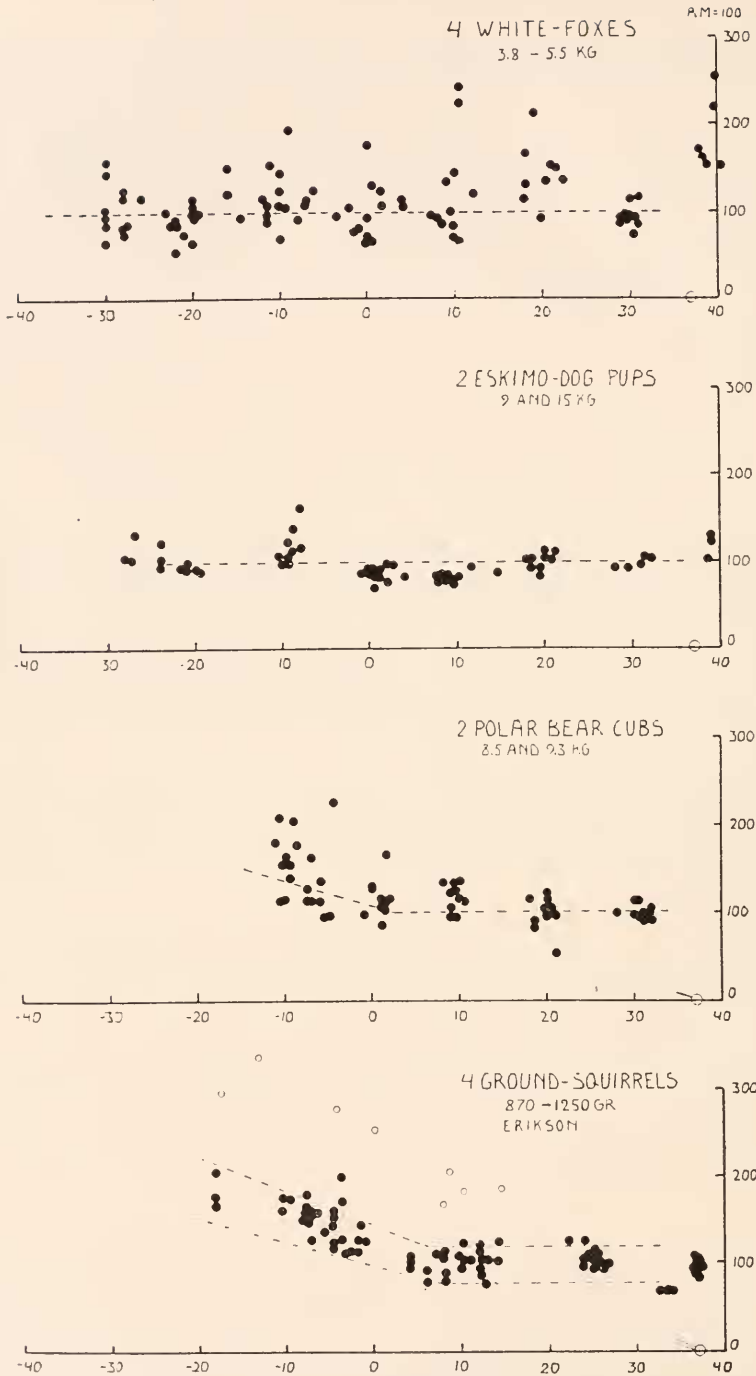
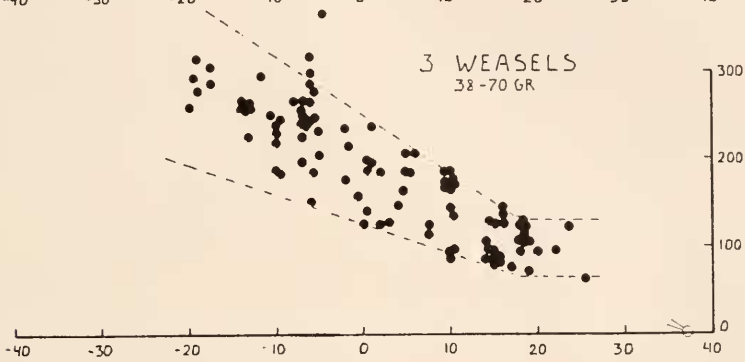
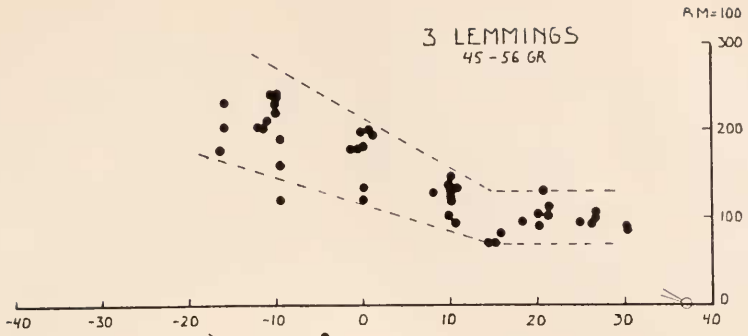


FIGURE 4. Metabolic heat regulation in arctic mammals. In the foxes and husky pups thermoneutrality extends from +30° C. to at least -30° C. The open circles in the ground squirrel plot (Erikson, 1950) indicate very active runs where the animal tried to escape.

# ARCTIC MAMMALS



# ARCTIC BIRDS

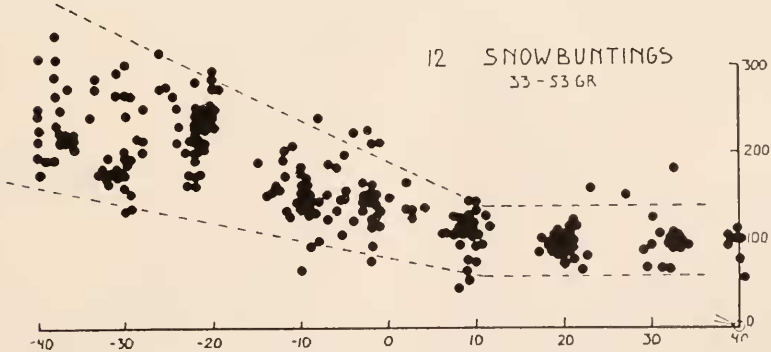
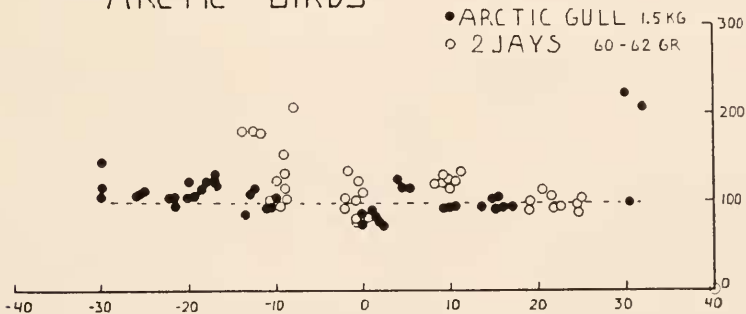
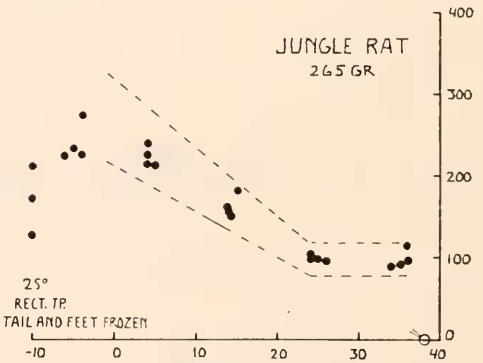
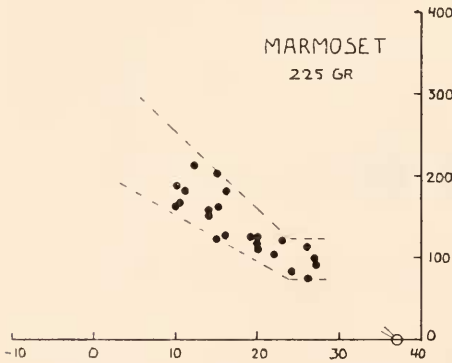
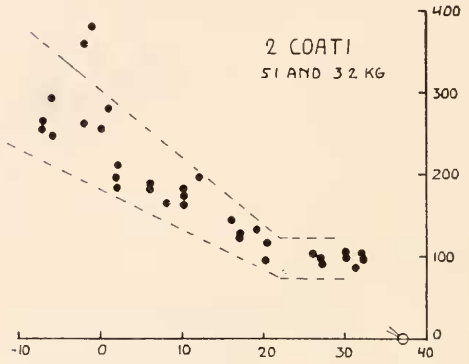
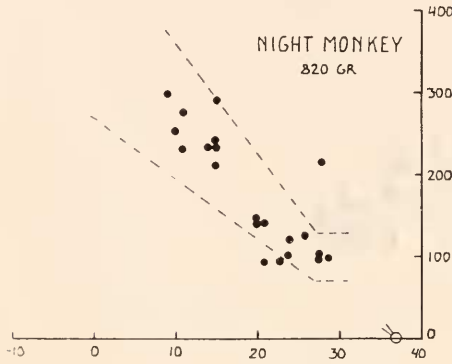
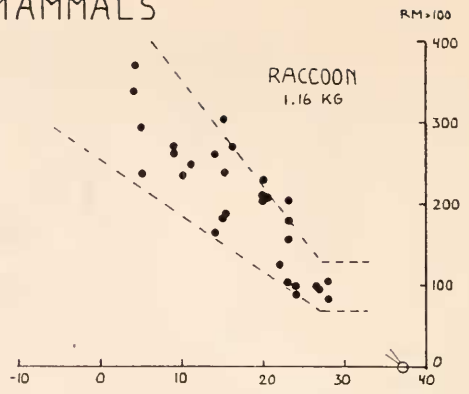
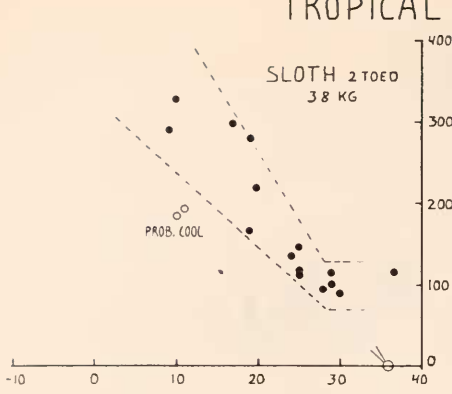
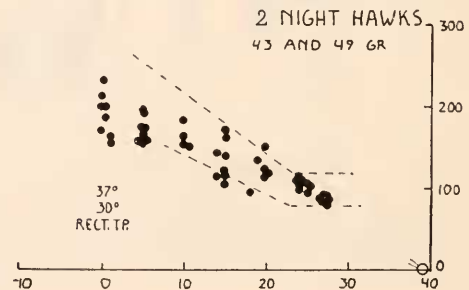
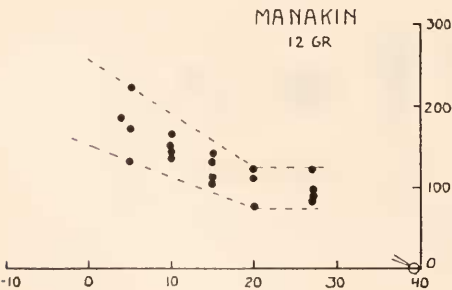


FIGURE 5. Metabolic heat regulation in small arctic mammals and in arctic birds.

# TROPICAL MAMMALS



# TROPICAL BIRDS





In Panama, it was established that the tropical mammals and birds responded with an increase in metabolism starting at only a few degrees below the ambient air temperature, producing strikingly steep curves compared with those of the arctic animals (Fig. 2). Such differences in slope had been observed by Lapique (1921) in different animals, and the curves were considered by him to flatten out with increase in size of the animal (Brody, 1945). The relation to size does not hold for the three animals given in Figure 2, however, for the steep-curved tropical raccoon is many times heavier than the little flat-curved arctic lemming. It might be assumed that the curves would become less steep with increasing insulation. However, the tropical raccoon has about the same insulation as the arctic lemming but has a much steeper curve. Altogether contrary to the assumption that insulation alone determines the slope, is the fact that a sloth has a much steeper curve than the less well insulated arctic weasel (Figs. 5 and 6).

Some simple physical considerations lead to an explanation which fits the facts surprisingly well and which also explains, for instance, how an arctic animal can endure temperatures that occasionally may drop as low as  $-70^{\circ}$  C. A physical analogy or model is useful to clarify what seem to be the main points.

Let us consider a warm-blooded animal as a unit capable of maintaining a constant body temperature in a changing environmental temperature, and that it can do this by adjusting (1) its insulation and (2) its metabolism. The major part of the metabolic increase which a mammal or bird can mobilize against external cooling results from muscular movements in the form of shivering and gross activity. We shall, therefore, picture our warm-blooded animal as an electric motor enclosed in an insulated bag. We shall assume a constant surface area and configuration of the bag and we shall maintain the interior of the bag at body temperature, say  $40^{\circ}$  C., by regulating the energy input to the motor. We are only studying situations of steady-state heat equilibrium where rate of heat loss equals rate of heat production. It has long been known that the overall heat loss of such a system in a uniform air current is proportional to the temperature gradient between the inside and the outside, according to Newton's law of cooling (Mitchell, 1901). That this also holds true in still air with considerable accuracy is evident from experiments by Burton, 1934 ( $16^{\circ}$  gradient), and by Winslow, Gagge, Greenburg, Moriyama and Rodee, 1935 ( $27^{\circ}$  gradient), and from numerous experiments with heated clothing dummies (copper man). According to the radiation law of Stefan (McAdams, 1942) we should expect, with increasing gradients, progressively smaller values than those predicted from Newton's law. However, as the surface of a good insulator (such as the fur in our arctic animals) progressively cools with the environmental temperature, we are mostly dealing with surface to air gradients which hardly exceed  $10-20^{\circ}$  and the calculated discrepancy for such small gradients is negligible, especially when compared with the great variation found in our animal experiments. In the present connection, therefore, Newton's law of overall cooling of physical

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FIGURE 6. Metabolic heat regulation in tropical mammals and birds. In most of them there is a fair proportionality to the body-to-air gradient. At the lowest temperatures the metabolism dropped in the jungle rat and the night hawks, as a result of falling body temperature. The two circles in the sloth plot were the last determinations and the animal was undoubtedly cool (no body temperature taken).

bodies can be applied as a natural basis for discussing the overall heat loss of animated bodies at different temperature gradients.<sup>7</sup>

Our heat regulating model is pictured in Figure 3, showing an electric motor (fan) in an insulated bag and a diagram relating the energy input necessary to maintain a constant body temperature for different gradients and insulations.

For a given insulation value (1) of the system the energy input for different temperature gradients ( $\Delta T$ ) would follow the diagonal (Ins. = 1), starting with zero energy at zero gradient. If the total insulation were twice as good, the rate of heat transfer would be only half and the energy input would consequently be only half, as indicated by the diagonal (Ins. = 2). Similarly with four times as good an insulation the rate of energy input would be one quarter as great as one and would be represented by the diagonal (Ins. = 4).

Now let us assume that our model, like the animals, can regulate its insulation and that it has a basal level below which the energy production does not fall. We shall further assume that the thermoregulation in our model always proceeds according to the following sequence when the external temperature falls: first, a gradual increase in the insulation alone until it has reached its maximum and thereafter a gradual increase in the energy input. In an animal the first part would correspond to: a zone of physical heat regulation, which at the critical temperature would change into the second part: the zone of metabolic (chemical) heat regulation, *i.e.*, we presume a complete separation between the physical and chemical heat regulation. Suppose now that we start with our model in air at +30° C. As we lower the temperature we increase the insulation correspondingly, running horizontally, until we reach 20° C. air temperature. If the insulation is then at its maximum (Ins. = 1) the curve will break and the energy input will increase proportionally to the gradient according to the diagonal marked Ins. = 1. If, however, the insulation can be steadily increased to a value of 2, the critical temperature will be at 0° C. and the energy input will, from then on, follow the line marked Ins. = 2. Similarly if the insulation can be increased 4 times and no more, the critical temperature will move to -40° C. and from then on the energy input will again be proportional to the gradient and will follow the diagonal marked Ins. = 4.

We have, according to convention, called the lowest temperature at which our model or animal can maintain body temperature without increasing metabolism, its critical temperature ( $TC$ ), and we shall designate the corresponding temperature gradient between body and environment as the critical gradient ( $\Delta TC$ ). In other words, critical gradient is the greatest temperature gradient which the physical heat regulation alone can take care of.

It will be seen from the Figure that the critical gradient for any given energy level is directly proportional to the insulation. If a system (Ins. = 1) has a critical gradient of 20° C. and is at 20° C. air temperature, doubling the insulation would double the critical gradient and move the critical temperature to 0° C. If another system (Ins. = 2) has its critical temperature at 0° C. and doubles its insulation, the critical gradient will double and the critical temperature move out to -40° C. Similarly, if a system with a fixed energy level can maintain a constant body tem-

<sup>7</sup> Dr. Alan C. Burton has kindly informed us that the theoretical drop from linearity by the radiation equation in actuality is counteracted by an increase in convection loss due to increased heat capacity as air gets cooler.

perature of 37° C. in an environmental temperature that changes from + 30° C. to - 40° C., as an arctic fox or dog can do, then we know that the gradient increased from 7° C. to 77° C. and hence that the insulation also increased by the same amount, namely, 11 times!

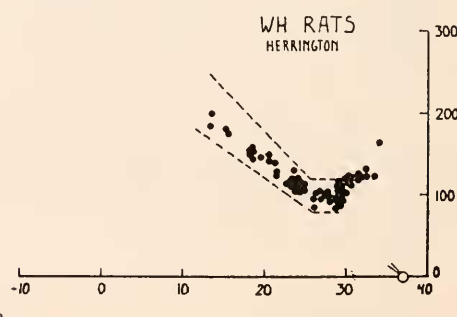
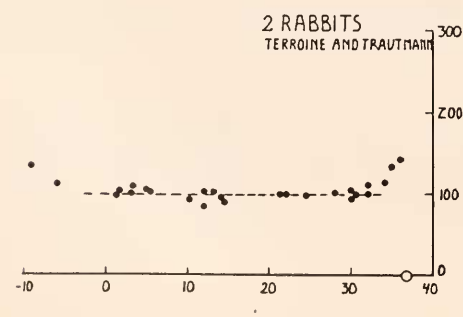
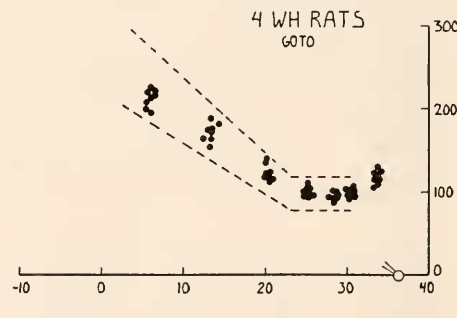
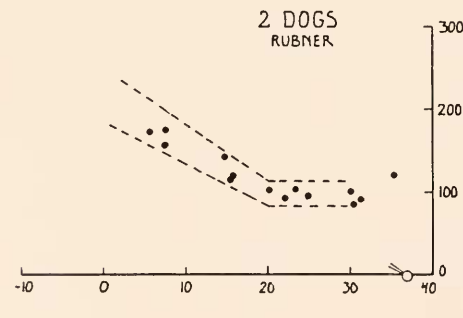
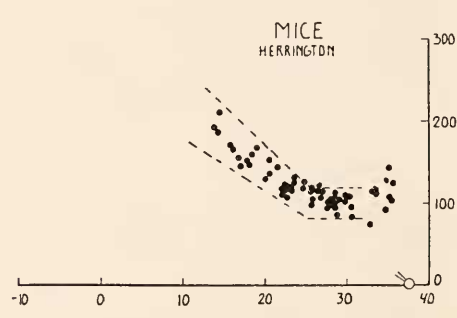
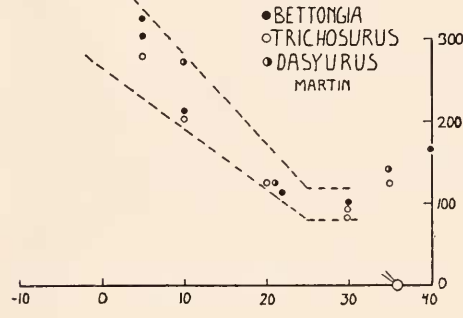
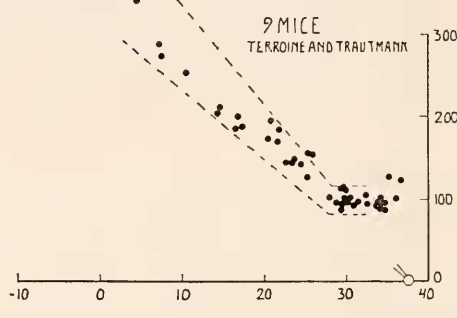
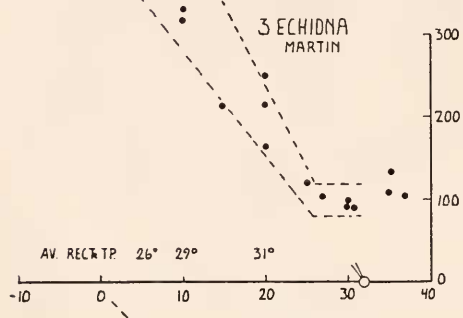
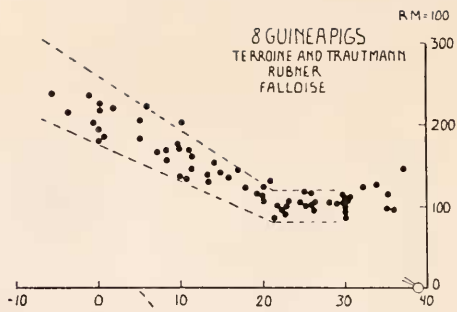
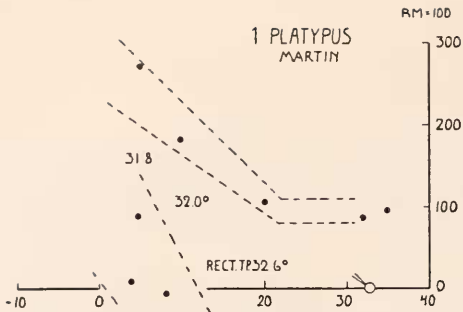
If we now consider the three systems (Ins. = 1, 2, and 4) and we double the energy level in all of them (from 100 to 200) we see that the critical gradient ( $\Delta TC$ ) will also double in each case; in other words, the critical gradient is proportional to the energy level. Physiologically this is of considerable interest. Doubling the metabolism in each system will move the critical temperature of Ins. = 1 from 20° C. to 0° C., of Ins. = 2 from 0° C. to - 40° C., and of Ins. = 4 from - 40° C. to - 120° C.! An arctic fox with body temperature of 40° C. and a critical temperature at - 40° C. can, merely by doubling its metabolism, go to - 120° C., and it takes only a 37 per cent increase in heat production to sustain it in the coldest temperature recorded on earth, somewhere near - 70° C.

The dependence of the critical gradient on the metabolism and the overall insulation can be combined in a simple formula: stating that the critical gradient is proportional to the product of the basal metabolism and the maximal overall insulation, or  $\Delta TC = K \times I \times E$ , where  $\Delta TC$  is the critical gradient,  $K$  is a constant denoting the units,  $I$  is the maximal overall insulation of the system and  $E$  is the basal energy level. As we shall see, this explains why a sloth, with a greater fur insulation than the arctic weasel and lemming and our other tropical animals, is still one of the most temperate sensitive animals because of its well known low metabolism.

We have now discussed some fundamental properties of a simple thermoregulated system with only two variables, insulation and metabolism. Our next task is to see to what extent we can expect this analogy to be applicable to a homoiothermic animal. Most authors (Hoesslin, 1888; Lefevre, 1911; Terroine and Zunz, 1925; DuBois, 1936) have emphasized the observation that heat loss from a warm-blooded animal is not proportional to the temperature gradient, and generally speaking this is true. The matter has been somewhat confused, however, by the failure to realize that proportionality should only hold below the critical temperature. Dahr (1926) cites the case of a guinea pig experiment of Rubner's as evidence that they lost heat according to Stefan's law of radiation, but uses body temperature instead of surface temperature. Actually his example nicely illustrates a linear relation to the body gradient. Martin (1902) points out that the heat production of Echidna is proportional to the gradient. Lapique (1921) and Kleiber and Dougherty (1934) assume, for theoretical reasons, an approximate applicability of Newton's law of cooling below the critical temperature, but do not furnish any factual evidence for it.

To what extent Newton's law would hold below the critical temperature depends upon several factors, the most important being (1) the constancy of the body temperature, (2) the degree of constancy of the overall insulation below the critical temperature, and (3) the degree of constancy of the heat production for each temperature. We shall discuss these factors below.

1. *Body temperature.* Generally speaking, the least variable factor in the whole picture of homoiothermy is the body temperature (Wetmore, 1921; Wislocki, 1933). The poorest temperature regulators are bats, which in the resting state are practically poikilothermous (Hock, 1949). Relatively poor regulators are the mono-



tremes Platypus and Echidna (Martin, 1902) and the Xenarthra, among which are the sloths and armadillos (Wislocki and Enders, 1935). Practically all others regulate to within  $\pm 1^\circ$ . However, when exposed to decreasing external temperature the central or main body temperature will finally fall, resulting in a relative lowering of the metabolism which drops from the line of proportionality. This is well illustrated in the three series of rat experiments of Gelineo replotted in Figure 8, and occurs in our jungle rat and night hawks (Fig. 6), and in Kendeigh's sparrows (Fig. 9), but is not apparent in Martin's Echidna (Fig. 7). Any change of insulation involves establishment of new temperature gradients and hence some change in the stored heat of the body. In large and well insulated animals, *e.g.*, man in heavy clothing, this may introduce considerable time lag before the new equilibrium is reached. All our animals were relatively small and the arctic ones, especially, were given considerable time for equilibrium.

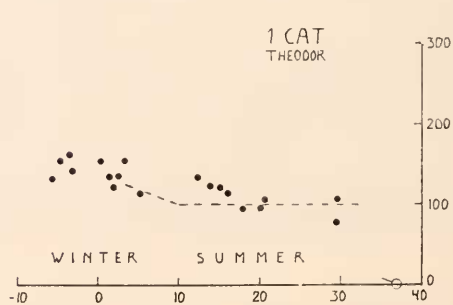
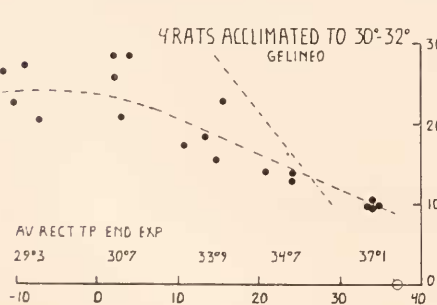
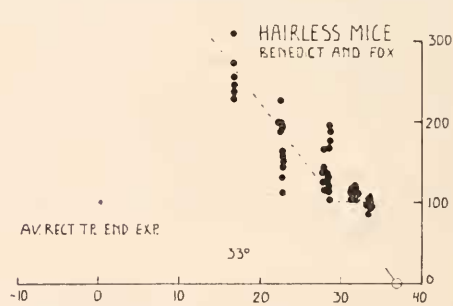
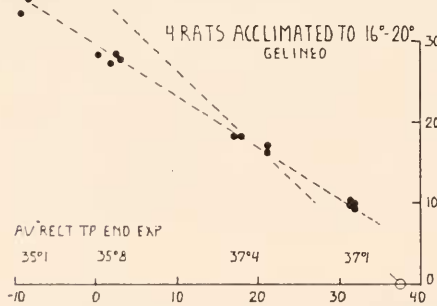
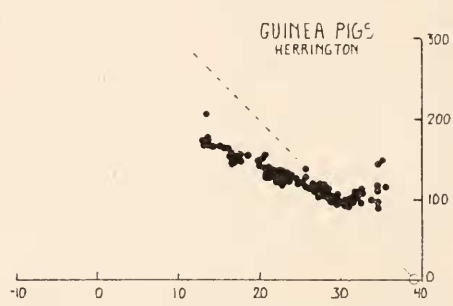
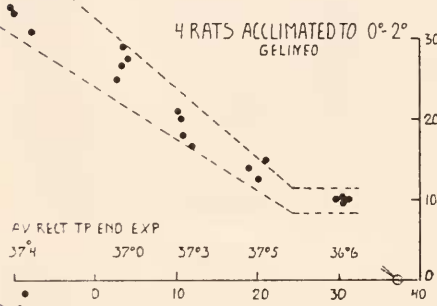
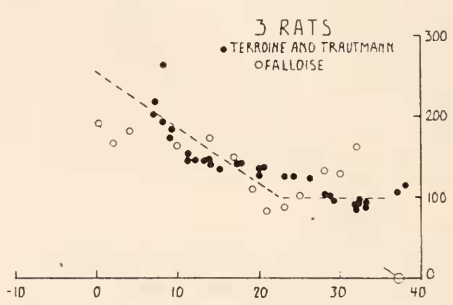
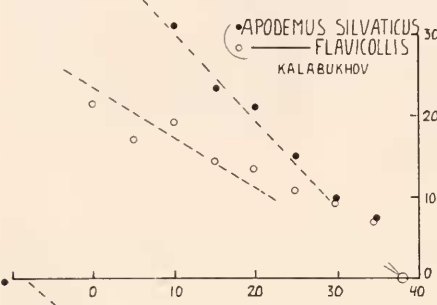
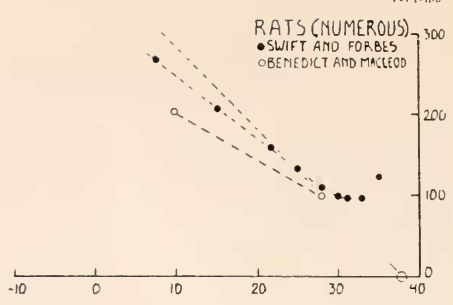
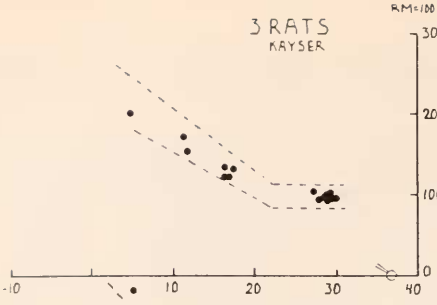
2. *Insulation.* Insulation here means the sum total of all factors, such as fur, skin and tissue cooling, and posture, that impede the loss of heat from the animal. In order to obtain proportionality between heat production and temperature gradient below the critical temperature, the insulation must remain constant at its maximum value. This, however, is only approximate. During an experiment the animals make various changes in posture. They have periods of activity which not only influence the energy output, but also the overall insulation. In the numerous experiments where each curve is based on many animals, considerable spread of data can be expected because different individuals may have different critical temperatures. Furthermore, if the experiments have been conducted over a long period of time involving seasonal changes in the animals' insulation (moulting), we must expect only poor correlation (Theodor's cat, Fig. 8).

In all animals the insulation cover over different parts of the body varies within wide limits. Provided, however, that each of these parts at the critical temperature has developed and maintains its individual maximum insulation, it will essentially, from then on, lose heat in proportion to the gradient according to Fourier's law (McAdams, 1942), and hence Newton's law of cooling would still apply for the whole animal. As we shall see, Newton's law of cooling does hold pretty well for the whole animal below the critical temperature, and apparently each external part of the body is able to maintain a maximal insulation and a certain minimum temperature until the environmental temperature drops too low for maintenance of the body temperature. This is also indicated by the observations on the gull's feet mentioned in the previous paper.

3. *Heat Production.* The extra heat production required to maintain the body temperature below the critical temperature is mainly derived from muscular metabolism, either as shivering, gross activity, or both. It is essentially discontinuous, occurring in bursts, and as the animals may also have other reasons to move about during the experiments we must accordingly expect a considerable spread of data. It should be emphasized that our animals were confined in relatively small cages so

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FIGURE 7. Metabolic heat regulation in mammals recalculated from literature. There is a fair overall adherence to Newton's law of cooling below the critical temperature. The echidna shows fair proportionality to gradient in spite of falling body temperature.



that they could not perform any normal exercise in order to keep warm, like running around. This undoubtedly curbs their heat production and gives a false impression of their full natural capacity for metabolic heat regulation.

### EXPERIMENTAL RESULTS

All of our own data, and all data from the literature that are sufficiently detailed, have been computed relative to a basal metabolic level in the thermo-neutral zone which we call 100, and are presented in Figures 4 through 9. Wherever possible, lines have been drawn according to the ideas put forth in Figure 3, so as to best fit the experimental data. It is evident that in the great majority of cases, going from arctic through temperate to tropical mammals and birds, the data fit the theory quite well. For a number of animals, especially in the arctic (fox, eskimo dog, polar bear, ground squirrel, arctic gull, snow bunting) and temperate regions (dog, rabbit, guinea pig, and goose), we see that there is a well defined zone of thermoneutrality extending in some of them down to  $-30^{\circ}$  C. This means that the insulation alone has compensated for the increasing gradient by a steady increase. From the observation that arctic dogs, foxes, and gulls sleep on the snow at  $-40^{\circ}$  C. to  $-50^{\circ}$  C.,

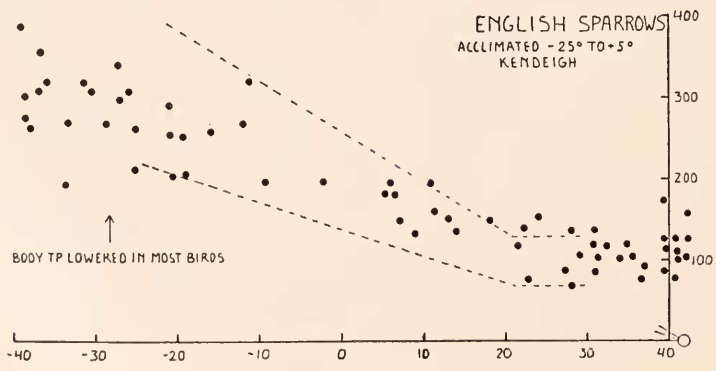
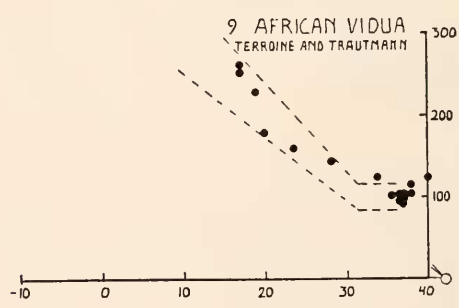
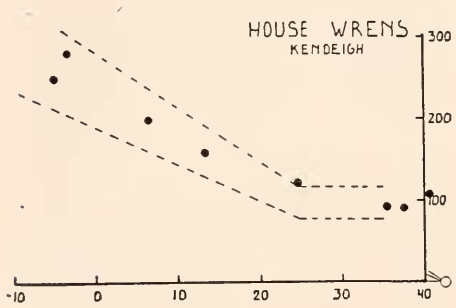
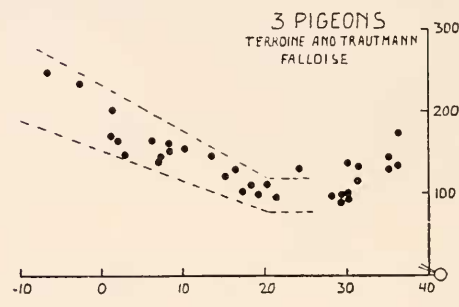
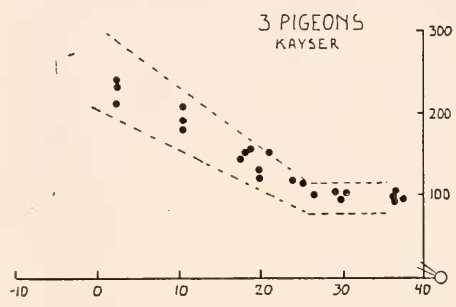
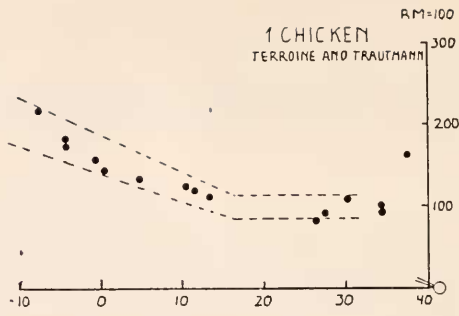
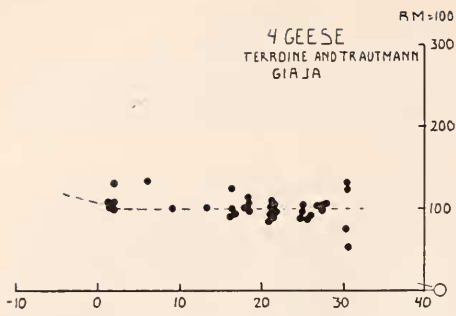
TABLE I

*Simultaneous temperature measurements in adult eskimo dogs  
(All temperatures Centigrade)*

Dog	A	B	C	D	E
Rectal	38.3	38.3	38.2	38.4	40
Subcutaneous	37.2	37.1	37.6	37.4	38.2
Surface of skin	33	36	36.7	35.4	30.0
Outer limit of fur	10	6 to 13	26	23	-10
Air	-3	-3	-3	-3	-19

it is likely that their zone of thermoneutrality extends at least that far, which means that their changing heat dissipation alone can balance the heat loss from  $+30^{\circ}$  C. to  $-40^{\circ}$  C. If the foxes' body temperature is  $37^{\circ}$  C. this is equivalent to an 11-fold change in temperature gradient, and hence they can produce an 11-fold change in heat dissipation in spite of being confined in a small cage. Conversely of course, it follows that at  $-40^{\circ}$  C. they can increase their heat loss by at least eleven times the basal heat production in order to get rid of heat produced while running. While running freely they can probably dissipate heat considerably better, which may be very important at less severe temperatures. In other words, from their extended zone of thermoneutrality it directly follows that they are equally amazing in ability to dissipate heat. A major factor in this ability must be vasodilatation and rise of skin temperature. An observation on eskimo dogs brought this out clearly. At  $-3^{\circ}$  C. air temperature the dogs could maintain a fur surface temperature, for some time, as high as  $+26^{\circ}$  C. (Table I). An eskimo dog that was brought to the States

FIGURE 8. Metabolic heat regulation in mammals recalculated from literature. The metabolic rate drops off with falling body temperature in Gelineo's acclimation experiments. In the large rat series by Benedict and MacLeod and the guinea pig series by Herrington there is a poor correlation to the gradient.





in the heat of the summer got rid of his heat by stretching out on his back, exposing his thinly haired abdomen, and panting vigorously. The observed magnitude of change of heat dissipation in the fox matches the observation by Brody and Cunningham (1936) that the maximum steady state of muscular activity in man and horse is of the order of 10–15 or even 20 times the resting metabolism. It was pointed out in the previous paper that the poorly insulated legs of the arctic mammals and birds are probably a major factor in the heat regulation of these animals.

In most of the tropical animals the zone of thermoneutrality is so limited and transitory that the two parallel lines drawn in the diagrams represent more of an abstraction than a reality. In some cases the transition between the zone of thermoneutrality and metabolic rise is definitely a curve (see Goto's rats, Herrington's mice, Fig. 7). Such a thing would happen also in our insulated model if the metabolic rise started before the maximum of the insulation had been reached. This may be a reason for the low slope in the rat experiments of Benedict and MacLeod and of Swift and Forbes (Fig. 8), and in the guinea pig experiments of Herrington (Fig. 8). Another reason may be a possible drop in body temperature at the lowest temperatures. Such a drop of the curves due to fall in body temperature is illustrated in Gelineo's rat experiments (Fig. 8), in Kendeigh's sparrows (Fig. 9), and in our jungle rat and night hawks (Fig. 6).<sup>8</sup> In the scant data on the platypus and the three Australian marsupials (Martin, Fig. 7), there is an upward trend in the curves. Because of the inherent spread in all similar experiments it seems doubtful that this trend is significant, but it could happen if the insulation deteriorated markedly with activity as may occur with human clothing.

As has been described, there is a considerable spread in most of the data and also a tendency to proportionately greater spread during the period of metabolic heat regulation, when bursts of activity rather than an even flow supply the heat which maintains the body temperature. The maximum amount of heat produced above the base value is undoubtedly influenced by time, and in long-time experiments the peak metabolism is seldom over 400 (Echidna) and usually not more than 300 per cent. In most cases, however, the high peak values (*metabolisme du sommet*) found after acute chilling in ice water (Giaja, 1925) cannot be produced in prolonged experiments. Animals at liberty to move about freely can, however, undoubtedly maintain a higher metabolic rate than under the cramped conditions of an experiment.

With the facilities available at the Arctic Research Laboratory at Point Barrow we were not able to reach the critical temperature for the foxes or dogs. However, with excellent cooperation from the Navy, two foxes and several snow buntings were flown to the Naval Research Laboratory, Washington, D. C., and a series of observations was made at temperatures down to  $-80^{\circ}$  C. (Table II). From the table it is apparent that  $-70^{\circ}$  C. induced shivering and is therefore below the critical temperature of the fox. He suffered no loss of body temperature after one hour's

<sup>8</sup> The drop in body temperature and poor metabolic response to the lowered outside temperature observed in this goatsucker may well be due to a hibernation reaction, as the related poor-will (*Phalaenoptilus nuttallii*) is known to hibernate (Amadon, 1949). This information was kindly furnished by Dr. R. C. Murphy of the American Museum of Natural History.

FIGURE 9. Metabolic heat regulation in birds recalculated from literature. Many of Kendeigh's sparrows drop off from the line of proportionality because of drop in body temperature, and many died after the severest cold exposure. *Vidua paradisica* (Terroine and Trautmann, 1927) is a bird native to equatorial West Africa (Delacour and Edmond-Blanc, 1933, 1934).

TABLE II

*Rectal temperature in white fox subjected to low temperature  
(All temperatures Centigrade)*

Air temp.	Duration in minutes	Rect. temp. before exp.	Rect. temp. end exp.	Remarks
+22		37°7		
-20		37°7		
-50	120	37-39°	37°6	Lying down asleep.
-60	105	37-39°	39°	Lying down asleep.
-70	90	39°	37°3	Licked feet ½ hour, curled up asleep, shivering after 1 hour.
-80	60	37-39°	38°	Licked himself, asleep, shivering after 5 minutes. Legs stiff, active.

stay at  $-80^{\circ}\text{C}$ ., and his metabolic heat regulation can probably balance considerably lower temperatures, but he may suffer local frost injury long before exhaustion of his metabolic resources. From observations of sleeping foxes and eskimo dogs it is believed that their critical temperature is somewhere between  $-45^{\circ}\text{C}$ . and  $-50^{\circ}\text{C}$ ., and it is most likely the same in all the other larger mammals of the same climate. Snow buntings, which normally migrate south in the winter, could not take  $-50^{\circ}\text{C}$ . and their body temperature dropped seriously within an hour.

The data on all our arctic and tropical animals are collected in charts, Figures 10 and 11, where the full drawn lines represent observations and the dotted lines represent extrapolation of the metabolism below a known critical temperature.

The animals most sensitive to low temperature have the steepest curves, with critical temperatures near the body temperature. The animals hardiest toward cold have the least slope, with critical temperatures farthest from the body temperature. We have noted that the cold hardiest animals, the fox and eskimo dog, can be expected to tolerate the coldest temperatures on earth merely by increasing their me-

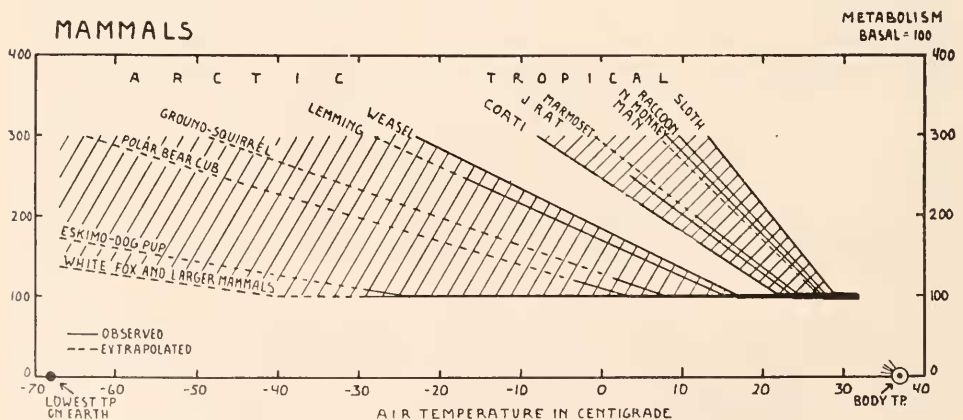


FIGURE 10. Heat regulation and temperature sensitivity in arctic and tropical mammals based on plots in Figures 4, 5, and 6. The fox needs only slight increase in metabolic rate to stand the coldest temperature on earth. The critical gradients (tp sensitivity) and the slope of the curves depend on the product of the basal metabolic rate and the overall body insulation.

tabolism 30–40 per cent, whereas the same increase in metabolism in a tropical animal will only help him by a few degrees.

The critical temperature in naked man is known to be around  $27^{\circ}\text{C}$ . (DuBois, 1936) to  $29^{\circ}\text{C}$ . (Winslow and Herrington, 1949), which places him among the more temperature sensitive of the tropical mammals. We have no data as to the critical temperature of Eskimos. They wear just as warm clothing as white men in the same environment, often warmer, and it is likely that the Eskimo is as sensitive to temperature as other people that wear clothing. Man is indeed a tropical animal carrying his tropical environment with him.

By using different amounts of clothing, tropical man can span the whole range from the tropics to the arctic and it could be assumed that his energy requirements below the critical temperature for each clothing assembly would essentially follow

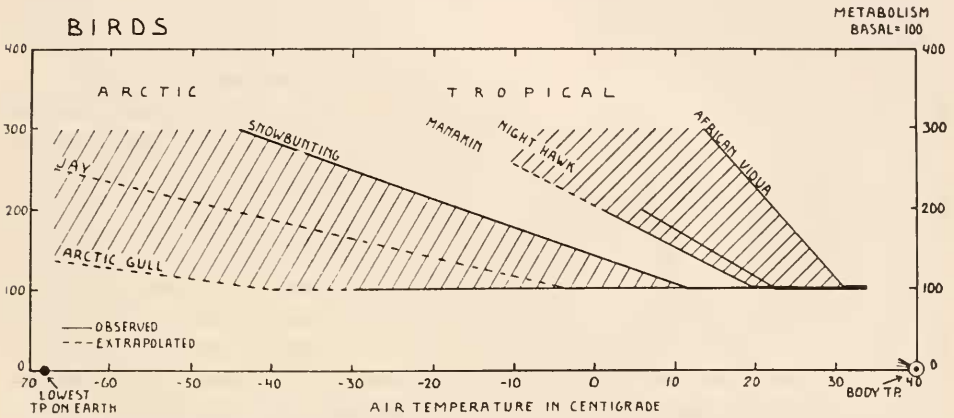


FIGURE 11. Heat regulation and temperature sensitivity in arctic and tropical birds, based on plots in Figures 5, 6, and 9.

Newton's law of cooling. It seems a challenge that we have been unable to unearth in the literature experiments in man, naked or clothed, with enough data to demonstrate adequately the thermoneutral zone and the slope of energy expenditure beyond it. In Figure 10 man's line below the critical temperature is hence dotted. It is known however, from studies at the Climatic Research Laboratory, Lawrence, Massachusetts, that the insulation value of clothing may drop considerably (50 per cent) during exercise (Belding, 1949, and personal communication), which would move the curves upward. Man cannot usually spend a night at  $-40^{\circ}\text{C}$ . in one-layer arctic fur clothing or naked in a one-layer arctic fur sleeping bag without getting cold and shivering. He needs more insulation than the animals whose fur he is using. The reasons may be several. In his outstretched sleeping position he exposes much more surface than an arctic mammal sleeping curled up. The arctic mammals may tolerate a low leg temperature, like the arctic gull, and thereby greatly conserve heat. Fur clothing and fur sleeping bags are usually not made from the heaviest winter fur, but rather from lighter autumn fur with less insulating value.

It is readily seen by comparing Figures 10 and 11 of this paper with Figure 3 in the preceding paper that the correlation between the measured insulation of a piece of fur of the animal and its temperature sensitivity does not hold in detail.

Thus the smaller arctic animals are considerably less temperature sensitive than the equally well or better insulated tropical mammals.

From Figure 3 it is clear that the temperature sensitivity, *i.e.*, critical gradient, depends upon the product of the overall insulation and the basal metabolic level. The overall insulation is only roughly reflected by measurements of the fur insulation on a patch taken from the body side or back, but even with this limitation we shall see that most of the apparent discrepancies can be explained by considering the metabolic level.

#### SUMMARY

A series of arctic and tropical mammals and birds at Point Barrow, Alaska (lat.  $71^{\circ}$  N.) and in Panama (lat.  $9^{\circ}$  N.) was subjected to various air temperatures in a respiration chamber where the heat production was determined by oxygen consumption or carbon dioxide production. The larger arctic mammals and birds showed no increase in metabolism at  $-30^{\circ}$  C. and from observations on sleeping animals it is probable that their zone of thermoneutrality extends to  $-40^{\circ}$  C. or  $-50^{\circ}$  C. The smaller arctic species show a high critical temperature and the tropical species even higher. Metabolic heat production increases rapidly with lowering of the temperature in a tropical mammal or bird, and slowly in an arctic animal. It can be shown theoretically that in a thermoregulated system with a fixed basal energy level and variable insulation the critical gradient is proportional to the maximal insulation and the basal energy level.

In a large series of experiments including our tropical and arctic animals, and all animals affording enough data in the literature, it is shown that the heat loss below the critical temperature is essentially proportional to the body-to-air gradient. This means that the overall insulation evidently reaches a maximum at the critical temperature and from then on the heat loss follows essentially Newton's law of cooling. It follows from this that an arctic mammal with a critical gradient of  $70^{\circ}$  C., by doubling its metabolism, theoretically would double the gradient. Only 40 per cent increase of its metabolism (or insulation) would suffice to take it down to  $-70^{\circ}$  C. which is near the lowest recorded temperature on earth.

The very broad zone of thermoneutrality in the larger arctic species, from  $+30^{\circ}$  C. to  $-40^{\circ}$  C., shows their ability to balance an 11-fold increase in gradient and hence the animal can change its heat dissipation by a factor of 11 even when lying down. It is believed that vasomotor control of the poorly insulated legs must play an important role in the general thermoregulation of these animals.

In the tropical mammals and birds the critical gradient is low, often only  $10^{\circ}$  C., which makes them sensitive to even small temperature changes. A  $10^{\circ}$  lowering of the air temperature from the critical temperature doubles the gradient for the tropical mammal; a  $9^{\circ}$  increase decreases the gradient 10 times, and in order to maintain the body temperature tropical animals must be able to adjust insulation and metabolism in the same proportion as the gradient. They are thus extremely sensitive to temperature changes.

The whole range of heat regulation from tropical to arctic mammals and birds is represented on two charts, Figures 10 and 11.

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## ADDENDUM

After the manuscript and illustrations were all prepared, Mr. Charles M. Bogert at the American Museum of Natural History kindly made us aware of an important paper appearing in the latest available issue of *Bulletin de l'Académie des Sciences de l'U.R.S.S.*, Volume 2, 1947, by R. P. Olmianskaya and A. D. Slonim. They subjected several zoo animals at Leningrad to temperatures from  $+20^{\circ}\text{C}$ . to  $-20^{\circ}\text{C}$ ., measuring metabolism and the rectal temperatures: *Vulpes vulpes*, *V. lagopus*, *V. melanotus*, *Lepus europaeus*, *L. timidus*, and *Nyctoreutes procyonoides*. The polar fox showed only insignificant rise in metabolism from  $+20^{\circ}\text{C}$ . to  $-20^{\circ}\text{C}$ ., the red fox a 50 per cent rise, and the other animals more. There is a fair correlation between gradient and metabolic rate in their curves. Absolute metabolic rates are not given. The authors conclude that the polar species have a more constant body temperature at low environmental temperatures than the southern species, and that the metabolism rises only little in the polar species as compared with the southern species. The maintenance of constant body temperature in the arctic species is considered to be due to an extraordinary vascular control. Insulation is not mentioned.

## LITERATURE CITED

- AMADON, D., 1949. Comments on recent literature. *The Wilson Bulletin*, **61**: 237.
- BELDING, H. B., 1949. Protection against dry cold. Quartermaster Climatic Research Lab., Rept. No. 155. Lawrence, Mass.
- BENEDICT, F. G. AND E. L. FOX, 1933. Der Energieumsatz normaler und haarloser Mäuse bei verschiedener Umgebungstemperatur. *Pflügers Arch. Gesamte Physiol.*, **231**: 455.
- BENEDICT, F. G. AND GRACE MACLEOD, 1929. The heat production of the albino rat. I. and II. *Jour. Nutrition*, **1**: 343 and 367.
- BRODY, S., 1945. Bioenergetics and growth. New York.
- BRODY, S. AND R. CUNNINGHAM, 1936. Growth and development, with special reference to domestic animals: XL. Comparison between efficiency of horse, man, and motor, with special reference to size and monetary economy. *Res. Bull. Agr. Exp. Sta.*, Univ. of Missouri, **244**: 5.
- BURTON, A. C., 1934. The application of the theory of heat flow to the study of energy metabolism. *Jour. Nutrition*, **7**: 497.
- DELACOUR, J. AND F. EDMOND-BLANC, 1933. Monographie des veuves. *Ois. Rev. Française Ornith.*, **3**: 3 and 4.
- DELACOUR, J. AND F. EDMOND-BLANC, 1934. Monographie des veuves. *Ois. Rev. Française Ornith.*, **4**: 1.
- DHAR, N. R., 1926. Influence of temperature on metabolism and the problem of acclimatization. *Allahabad Univ. Studies*, **2**: 313.
- DU BOIS, E. F., 1936. Basal metabolism in health and disease. Philadelphia.
- ERIKSON, H., 1950. Unpublished data.
- FALLOISE, A., 1900. Influence de la température extérieure sur les échanges respiratoires chez les animaux à sang chaud et chez l'homme. *Arch. Biol.*, **17**: 761.
- GELINEO, M. S., 1934. Influence du milieu thermique d'adaptation sur la thermogénèse des homéothermes. *Ann. Physiol. Physicochim. Biol.*, **10**: 1083.

- GIAJA, J., 1925. Le métabolisme de sommet et le quotient métabolique. *Ann. Physiol. Physicochim. Biol.* 1: 596.
- GIAJA, A., 1931. Contribution à l'étude de la thermorégulation des oiseaux. *Ann. Physiol. Physicochim. Biol.*, 7: 13.
- GOTO, K., 1923. Beitrag zur Kenntnis der chemischen Wärmeregulation der Säugetiere. *Biochem. Zeitschr.*, 135: 107.
- HERRINGTON, L. P., 1940. The heat regulation of small laboratory animals at various environmental temperatures. *Amer. Jour. Physiol.*, 129: 123.
- HOCK, R. J., 1949. Temperature and bat metabolism. Unpublished doctoral thesis, Cornell Univ.
- HOESSLIN, H. v., 1888. Über die Ursache der scheinbaren Abhängigkeit des Umsatzes von der Grösse der Körperoberfläche. *Arch. Anat. Physiol., Physiol. Abth.*, p. 323.
- KALABUKHOV, N. I., 1940. Influence of temperature upon oxygen consumption by wood-mouse (*Apodemus sylvaticus* L.) and yellow-necked mouse (*A. flavicollis* Melch.). *Compt. Rendus Acad. Sci. URSS*, 26: 89.
- KAYSER, C., 1930. Contribution à l'étude de la régulation thermique. *Ann. Physiol. Physicochim. Biol.*, 6: 721.
- KAYSER, C., 1937. Variations du quotient respiratoire en fonction de la température du milieu chez le rat, le pigeon et le cobaye. *Compt. Rendus Soc. Biol.*, Paris, 126: 1219.
- KENDEIGH, S. C., 1939. The relation of metabolism to the development of temperature regulation in birds. *Jour. Exp. Zool.*, 82: 419.
- KENDEIGH, S. C., 1944. Effect of air temperature on the rate of energy metabolism in the English sparrow. *Jour. Exp. Zool.*, 96: 1.
- KLEIBER, M. AND J. E. DOUGHERTY, 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. *Jour. General Physiol.*, 17: 701.
- LAPICQUE, L., 1921. Échanges nutritifs des animaux en fonction du poids corporel. *Compt. Rendus Acad. Sci.*, Paris, 172: 1526.
- LEFÈVRE, J., 1911. Chaleur animale et bioénergétique. Paris.
- McADAMS, W. H., 1942. Heat transmission. New York.
- MARTIN, C. J., 1902. Thermal adjustment and respiratory exchange in monotremes and marsupials. *Phil. Trans. Roy. Soc. London, B*, 195: 1.
- MITCHELL, A. C., 1901. On the convection of heat by air currents. *Trans. Roy. Soc. Edinburgh*, 40: 39.
- OLNIANSKAYA, R. P. AND A. D. SLONIM, 1947. On the adaptability of animal organisms to very low temperatures of the environment. *Bull. Acad. Sci. URSS*, ser. Biol., 2: 245.
- RUBNER, M., 1902. Die Gesetze des Energieverbrauches bei der Ernährung. Berlin-Wien. (Quoted from OTTO KESTNER AND RAHEL PLAUT, Physiologie des Stoffwechsels, in H. Winterstein, *Handbuch der Vergleichenden Physiologie*, 2: 901, 1924. Jena.)
- SCHOLANDER, P. F., 1947. Analyzer for accurate estimation of respiratory gases in one-half cubic centimeter samples. *Jour. Biol. Chem.*, 167: 235.
- SWIFT, R. W. AND R. M. FORBES, 1939. The heat production of the fasting rat in relation to the environmental temperature. *Jour. Nutrition*, 18: 307.
- TERROINE, E. F. AND S. TRAUTMANN, 1927. Influence de la température extérieure sur la production calorifique des homéothermes et loi des surfaces. *Ann. Physiol. Physicochim. Biol.*, 3: 422.
- TERROINE, E. F. AND E. ZUNZ, 1925. Le métabolisme de base. Les Presses Universitaires de France, Paris.
- THEODOR, C., 1878. Über den Einfluss der Temperatur der umgebenden Luft auf die Kohlen-säureausscheidung und die Sauerstoffaufnahme bei einer Katze. *Zeitschr. Biol.*, 14: 51.
- WETMORE, A., 1921. A study of the body temperature of birds. *Smithsonian Misc. Coll.*, 72 (12): 1.
- WINSLOW, C. E. A., A. P. GAGGE, L. GREENBURG, I. M. MORIYAMA AND E. J. RODEE, 1935. The calibration of the thermo-integrator. *Amer. Jour. Hygiene*, 22: 137.
- WINSLOW, C. E. A. AND L. P. HERRINGTON, 1949. Temperature and human life. Princeton.
- WISLOCKI, G. B., 1933. Location of the testes and body temperature in mammals. *Quart. Rev. Biol.*, 8: 385.
- WISLOCKI, G. B. AND R. K. ENDERS, 1935. Body temperatures of sloths, anteaters, and armadillos. *Jour. Mammal.*, 16: 328.